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Sigwart, J., & Schwabe, E. (2017). Anatomy of the many feeding types in polyplacophoran molluscs. *Invertebrate Zoology*, 14(2), 205–216. <https://doi.org/10.15298/invertzool.14.2.16>

Published in:
Invertebrate Zoology

Document Version:
Publisher's PDF, also known as Version of record

Queen's University Belfast - Research Portal:
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This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No H2020-MSCA-IF-2014-655661.

Anatomy of the many feeding types in polyplacophoran molluscs

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ABSTRACT: Seven different ecological feeding strategies have previously been identified among chitons, despite their apparent morphological homogeneity. These include: detritivores, herbivores, omnivorous grazers, carnivorous grazers, specialist spongivores, epizoophagous feeders, xylophagous wood-dwelling species and true predators. The majority of species among common intertidal chitons appear to be omnivorous grazers. Here, we examined the gut morphology, and radula morphology, in species from various feeding types. The proportionate length and mineralization of the radula are not strongly correlated with feeding type, but these characteristics could be refined and later used to exclude particular habits where no other ecological data are available. Gut length in chitons follows classical gut foreshortening, with ambush predators having a short intestinal tract forming a single major loop, whereas obligate herbivores having dramatically long intestinal lengths with multiple coilings. Multiple feeding strategies, and concomitant adaptation of the digestive system, can be observed among phylogenetically closely-related taxa. Niche partitioning through dietary specialization, even among co-occurring omnivorous grazers, may speculatively underpin the success of chitons in the Northeast Pacific and other regions.

How to cite this article: Sigwart J.D., Schwabe E. 2017. Anatomy of the many feeding types in polyplacophoran molluscs // *Invert. Zool.* Vol.14. No.2. P.205–216. doi: 10.15298/invertzool.14.2.16

KEY WORDS: gut length, morphology, carnivore, omnivore, herbivore.

Приспособление гастральной системы хитонов к различным типам питания

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РЕЗЮМЕ: Вопреки морфологическому единообразию хитонов, семь типов пищевого поведения было описано у представителей этой группы. Среди хитонов известны виды детритофаги, растительноядные, всеядные, плотоядные, специализированные

поедатели губок, поедатели эпибионтов, виды, питающиеся древесиной, и настоящие хищники. Большинство типичных литоральных хитонов являются всеядными организмами. В настоящей работе мы изучили морфологию кишечника и строение радулы у представителей хитонов с разным пищевым поведением. Относительная длина радулы и минерализация ее зубов строго не коррелируют с типом питания, однако, эти морфологические признаки могут быть использованы для понимания биологии вида. Длина кишечника у хитонов следует типичной схеме и изменяется в зависимости от типа питания. Так, у хищников засадчиков короткий кишечный тракт образует только одну петлю, тогда как растительноядные хитоны имеют потрясающе длинный кишечник, формирующий несколько петель. Сходные стратегии пищевого поведения и связанные с ними адаптации пищеварительной системы могут быть выявлены у близкородственных групп. Разделение экологических ниш по особенностям диеты даже среди сосуществующих всеядных хитонов может рассматриваться как основа биологического прогресса группы северо-восточной Пацифики и других регионах.

Как цитировать эту статью: Sigwart J.D., Schwabe E. 2017. Anatomy of the many feeding types in polyplacophoran molluscs // *Invert. Zool.* Vol.14. No.2. P.205–216. doi: 10.15298/invertzool.14.2.16

КЛЮЧЕВЫЕ СЛОВА: протяженность кишечника, морфология, плотоядность, всеядность, растительноядность.

Introduction

Polyplacophoran molluscs (chitons) have persisted since the Carboniferous with little change in morphology (Sirenko, 2006). Living chitons are characterised by eight overlapping dorsal shell valves, surrounded by a fleshy girdle and covering a ventral creeping foot. The morphological variation in shell sculpture, girdle ornamentation and the radula are traditionally the main features used to differentiate taxa (Schwabe, 2010).

Chitons can be locally abundant and exert top-down control on their habitats (Dethier, Duggins, 1984). Littler and Littler (1999) demonstrated that the structure of the food source (in that case, algae) may change considerably due to the feeding activities of *Cryptoplax larvaeformis* (de Blainville MS, Burrow, 1815). Thus what chitons eat, is of significant importance not only to understanding the natural history of the animals, illuminating metabolic demand (Williams et al., 2001) and the accurate reconstruction of marine food webs.

While chitons are traditionally characterised as slow-moving algal grazers, there is an

increasing body of literature that demonstrates a broad variety of feeding types and much more complexity in the role of chitons in rocky intertidal food webs. Chitons usually scrape food from the substratum they inhabit by means of their iron-mineralized radula. Often several different organisms or even substratum particles may be found in the gut contents, and there is growing evidence that the majority of intertidal chitons are omnivorous browsers, capable of digesting animal and plant matter (Latyshev et al., 2004; Camus et al., 2009). By contrast, some species are selective feeders and are known to nip off small portions of whole-leaf seaweed (e.g. Putman, 1990).

True ambush predation has evolved separately in at least three different lineages of chitons: *Placiphorella*, *Loricella*, and *Craspedochiton* (Saito, Okutani, 1992). This behaviour was first observed by McLean (1962) demonstrating the feeding behaviour of *Placiphorella velata* Carpenter, Dall, 1879. This species and congeners possess a head region with an anteriorly extended mantle divided into tentacles. Although predatory, the animals are almost totally sessile and have an extremely low

metabolism (Carey et al., 2013). In its habitat, this species lies in wait of small prey such as crustaceans and polychaetes (see also Burghardt, 1979), with the anterior girdle uplifted and the precephalic tentacles pressed to the substratum. If a potential prey item touches the highly sensitive tentacles, the girdle flap can be lowered within a second to capture the victim, then feeding reportedly takes up to an hour. A similar strategy was reported for *Loricella angasi* (Adams, Angas, 1864) by Ludbrook and Gowlett-Holmes (1989), and also interpreted for two species of *Craspedochiton* by Saito and Okutani (1992). The digestive anatomy of these species is also apparently adapted for digesting a carnivore's diet, with a distinct short intestinal loop (Saito, Okutani, 1992).

Other species of chitons show additional feeding specialisms. Some species feed exclusively on sponges and can be interpreted as spongivorous (Warén, Klitgaard, 1991; Gowlett-Holmes, 2001; Schiaparelli et al., 2004). The feeding types of some species from chemosynthetic environments are still unclear and should be subject of future studies, for example *Trioplax balaenophila* (Schwabe, Sellanes, 2004), which was found on whale bones (Schwabe, Sellanes, 2004). Sirenko (2004) already pointed out that some chiton taxa may profit from the digestion support of symbiotic fungi or bacteria in their gut. This was confirmed for one species of chiton that lives on sunken wood, *Nierstraszella lineata* (Nierstrasz, 1905) with wood-digesting bacteria in its gut; however, another co-occurring species also on wood deposits lacks such bacteria and apparently grazes on superficial biofilms (Duperron et al., 2013).

Despite a number of publications dealing with the intestine or gut analysis of distinct species (e.g., Barnawell, 1960; Boolootian, 1964; Glynn, 1970; Demopulos, 1975; Nishi, 1975; Putman, 1990; Warén, Klitgaard, 1991; Saito, Okutani 1992; Schiaparelli et al., 2004), comparative studies are rare. After an analysis of more than 120 species, Sirenko (2000) grouped the animals according to their feeding behaviour in seven categories: detritivorous, herbivorous, omnivorous, carnivorous, epizooph-

agous, xylophagous and true predators. Interestingly, the different trophic groups correlate seemingly well with the ratio of the digestive tract length and the body size of the relevant species (Sirenko, 2004).

In this brief study, we have compiled some additional data to address comparative questions of diet variation among chitons at different taxonomic levels. The radula is an important feature for taxonomy and phylogeny (Saito, 2004). While individual teeth show significant species- and clade-level variation, the overall structure of the chiton radula is highly conserved relative to some other molluscan groups. Chiton radulae have 17 teeth per row in a conserved arrangement, dominated by the enlarged, iron-mineralized second lateral teeth. These major lateral teeth, mineralized with iron magnetite, are assumed to be adaptive to constant grazing on rock substrata (Lowenstam, 1962). Yet, such teeth are present in all living species of chitons, including those with the whole variety of feeding types reviewed above. We compiled quantitative data on radulae from across all seven feeding categories of chitons to investigate whether there is any pattern in tooth density, relative radular length, or the relative size of the radular cartilages, that might correlate to ecotype.

Separately, we re-examine the question of intestinal length. Although the gonad is known to vary in annual seasonal cycles in adult chitons, the length and shape of the intestinal tract does not change (Himmelman, 1976). Plate (1899, 1901) proposed a suite of morphological characters including gut morphology, but these have not been used extensively in the subsequent literature. Following the observations of Sirenko (2000, 2004) in comparing different feeding types, we selected representatives of a single taxonomic family that is known to have lineages adapted to multiple ecotypes in a relatively recent evolutionary radiation. The family Mopaliidae in the eastern Pacific encompasses a wide range of morphological forms, including the largest living chiton *Cryptochiton stelleri* (von Middendorff, 1847), which achieves body sizes in excess of 20 cm and has valves entirely

covered by tissue. Members of Mopaliidae also include a broad range of feeding ecologies: the predatory chiton *Placiphorella*, noted above, as well as specialist algal feeders (*Cryptochiton*) and generalist browsers (*Mopalia*). Examining the intestinal morphology and gut length of species within the superfamily Mopaliioidea provides a test of Sirenko's (2004) hypothesis that gut length is indicative of feeding type, and an opportunity to assess species-level differences in gut coiling among closely related taxa.

Material and methods

Species in the superfamily Mopaliioidea, many of which are common in the intertidal and shallow subtidal of the NE Pacific, are well represented in ecological literature, in particular the genera *Cryptochiton*, *Mopalia*, *Katharina*, *Placiphorella*, in Mopaliidae, and also *Tonicella* and *Cyanoplax*. These latter two genera are phylogenetically classified in a separate family, Tonicellidae, within the same superfamily (Sigwart et al., 2013).

To determine variation among feeding ecotypes, we examined intestinal morphology and length of the digestive tract in species in several genera in Mopaliioidea. A combination of fresh specimens and historical material from museum collections (Royal BC Museum, Victoria, Canada: RBCM) were dissected to examine the morphology of the intestinal tract. The organs of polyplacophorans molluscs are well differentiated, and the visceral cavity posterior of the stomach and digestive gland contains primarily the gonad in the dorsal part of the cavity, and the intestine, which is interspersed with nephridial tissues. The intestine is not differentiated into discrete sections but can be extensively coiled. The intestine was removed from the body cavity and uncoiled to directly measure the length. For one example in each species, *camera lucida* drawings of the intestinal morphology were converted to high-resolution vector graphics for purposes of illustration and to calculate gut dimensions. In total, gut morphology and length were examined for 162 specimens in 13 species in Mopaliioidea: *Cryp-*

tochiton stelleri (von Middendorff, 1847), *Katharina tunicata* (Wood, 1815), *Mopalia ferreirai* Clark, 1991, *M. hindsii* (Sowerby, Reeve, 1847), *M. kennerleyi* Carpenter, 1864, *M. lignosa* (Gould, 1846), *M. muscosa* (Gould, 1846), *M. spectabilis* I.M. Cowan and G.M. Cowan, 1977, *M. vespertina* (Gould, 1852), *Placiphorella velata* Carpenter MS, Dall, 1879, *Cyanoplax dentiens* (Gould, 1846), *Tonicella lineata* (Wood, 1815), *Plaxiphora albida* (de Blainville, 1825). The lattermost taxon, *Plaxiphora*, does not occur in the Northeast Pacific fauna and its placement within Mopaliioidea is equivocal (Sigwart et al., 2013).

To expand sampling of the morphological variation among all seven proposed feeding types of chiton (Sirenko, 2000), we obtained measurements of the radula from museum specimens of species with literature support for their classification in each dietary category (Bavarian State collection of Zoology, Munich: ZSM; Australian Museum; AM). It is impossible to provide all available data for the feeding behaviour of chitons, nevertheless, we compiled representatives of the major trophic groups with documented diets from ecological studies (Table 1). Radula data are not provided for all species of Mopaliioidea examined, to avoid sampling bias in favour of this clade or the subset of feeding types represented.

Results

We identified three types of generalised gut coiling morphology in the species of Mopaliioidea examined, which conform to herbivore, omnivore, and carnivore types. Concentric coiling seen in *Cryptochiton*, *Tonicella*, and *Plaxiphora* is apparently diagnostic for herbivory (Fig. 1). The proportional length of the gut (intestine: body length ratio) is not clearly divide into quantitative categories, and the proportional gut length of the three generalised morphologies exist on a continuous gradient (Figs 1, 2A). Quantitative metrics are presented only where there were multiple specimens where body length could be accurately measured, i.e. from specimens that were not curled (Fig. 2A).

Table 1. Example records of the feeding preferences of chiton species in all seven identified feeding types, and radula metrics. Feeding types are presented in the same sequence as illustrated in Fig. 2.

Species	Feeding type	Main food sources	References	RL/ BL	MT/ Tt	RL/ CL
<i>Loricella angasi</i> (Adams in Adams & Angas, 1864)	P	Amphipods	[4]	0.21	0.80	3.00
<i>Placiphorella stimpsoni</i> (Gould, 1859)	P	[specifics unknown]	[9]	0.28	0.81	1.84
<i>Placiphorella velata</i> Carpenter MS, Dall, 1879	P	Amphipods, polychaetes [aquarium experiments]	[2]			
<i>Chiton calliozonus</i> Pilsbry, 1894	O	Crustose coralline algae, bryozoans	[4]	0.35	0.82	2.82
<i>Chiton tricostalis</i> Pilsbry, 1894	O	Crustose coralline algae, bryozoans	[4]	0.29	0.86	3.04
<i>Cryptoplax striata</i> (Lamarck, 1819)	O	Seagrass, macroalgae, sponges	[4]	0.24	0.80	4.24
<i>Ischnochiton elongatus</i> (de Blainville, 1825)	O	Seagrass, ascidians	[4]	0.26	0.84	2.09
<i>Ischnochiton lineolatus</i> (de Blainville, 1825)	O	Seagrass, macroalgae, ascidians	[4]	0.28	0.86	2.28
<i>Lorica volvox</i> (Reeve, 1847)	O	Crustose coralline algae, sponges, serpulid polychaetes	[4] as <i>L. cimolia</i>	0.37	0.89	3.47
<i>Katharina tunicata</i> (Wood, 1815)	H / O	brown algae (<i>Hedophyllum</i>), green algae, small animals, diatoms	[5, 7]			
<i>Tonicella lineata</i> (Wood, 1815)	H	encrusting coralline algae, epiphytic diatoms	[7]			
<i>Callochiton crocinus</i> (Reeve, 1847)[1]	H	brown algae (Petroderma)	[4]	0.23	0.81	3.50
<i>Chiton diaphorus</i> (Iredale & May, 1916)	H	Crustose coralline algae	[4]	0.30	0.83	2.16
<i>Ischnochiton australis</i> (Sowerby, 1840)	H	Seagrass, macroalgae	[4]	0.30	0.85	2.23

Table 1 (continued).

Species	Feeding type	Main food sources	References	RL/ BL	MT/ Tt	RL/ CL
<i>Ischnochiton cariosus</i> Carpenter in Pilsbry, 1892	H	Seagrass, macroalgae	[4]	0.29	0.76	2.36
<i>Ischochiton torri</i> Iredale & May, 1916	H	Seagrass	[4]	0.26	0.84	2.35
<i>Plaxiphora albida</i> (de Blainville, 1825)	H	Filamentous algae, geniculate corallines	[4]	0.28	0.81	2.19
<i>Hanleya nagelfar</i> (Lovén, 1846)	S	Sponges (Geodiidae)	[8]	0.49	0.88	1.47
<i>Notoplax speciosa</i> (Adams, 1861)[1]	S	Sponges	[4, 10]	0.34	0.80	2.63
<i>Ferreiraella takii</i> (Wu & Okutani, 1984)	X	Wood	[12]	0.44	0.79	1.41
<i>Leptochiton vietnamensis</i> Sirenko, 1988	X	Wood	[12]	0.39	0.76	1.82
<i>Nierstraszella lineata</i> (Nierstrasz, 1905)	X	Wood, leaves	[12]	0.38	0.80	2.03
<i>Chaetopleura angulata</i> (Spengler, 1797)	C	Barnacles	[6]	0.41	0.81	3.03
<i>Ischnochiton smaragdinus</i> (Angas, 1867)	C	Sponges, ascidians	[4]	0.47	0.88	3.41
<i>Mopalia kennerleyi</i> Carpenter, 1864	C	invertebrates	[7]			
<i>Mopalia hindsii</i> (Sowerby MS, Reeve, 1847)	C	Barnacles, invertebrates	[1, 6]			
<i>Deshayesiella curvata</i> (Carpenter MS, Pilsbry, 1892)	E		[11]	0.39	0.82	2.63
<i>Oldroydia percrassa</i> (Dall, 1894)	E		[11]	0.53	0.85	2.97
<i>Mopalia muscosa</i> (Gould, 1846)	D?	diatoms, green algae	[7]			
<i>Cyanoplax dentiens</i> (Gould, 1846)	D	diatoms	[7]			
<i>Leptochiton asellus</i> (Gmelin, 1791)	D		[11]	0.53	0.80± 0.02 [13]	2.92

Table 1 (continued).

Species	Feeding type	Main food sources	References	RL/BL	MT/Tt	RL/CL
<i>Leptochiton algesirensis</i> (Capellini, 1859)	D		after [11]	0.57	0.68	4.13
<i>Leptochiton cancellatus</i> (Sowerby, 1840)	D		after [11]	0.43	0.79	2.60
<i>Stenosemus albus</i> (Linnaeus, 1767)	D / O	Protozoa, Chrysophyta, sponges, Arthropoda	O [3]; D, after [11]	0.40	0.79	2.40

Abbreviations: BL — body length, C — carnivorous, CL — length of the cartilage, D — detritivorous, E — epizoophagous, H — herbivorous, MT — number of rows with mineralized teeth, O — omnivorous, P — predator, RL — radula length, S — spongiovorous, Tt — total number of teeth rows, X — xylophagous.

References used in this compilation are noted in chronological order: 1 — Barnawell (1960), 2 — McLean (1962), 3 — Langer (1983), 4 — Kangas & Sheperd (1984), 5 — Dethier & Duggins (1984), 6 — Kaas & Van Belle (1985), 7 — Piercy (1987), 8 — Warén & Klitgaard (1991), 9 — Okutani & Saito (1992), 10 — Kaas et al. (1998), 11 — Sirenko (2000), 12 — Sirenko (2004), 13 — Sigwart and Carey (2014).

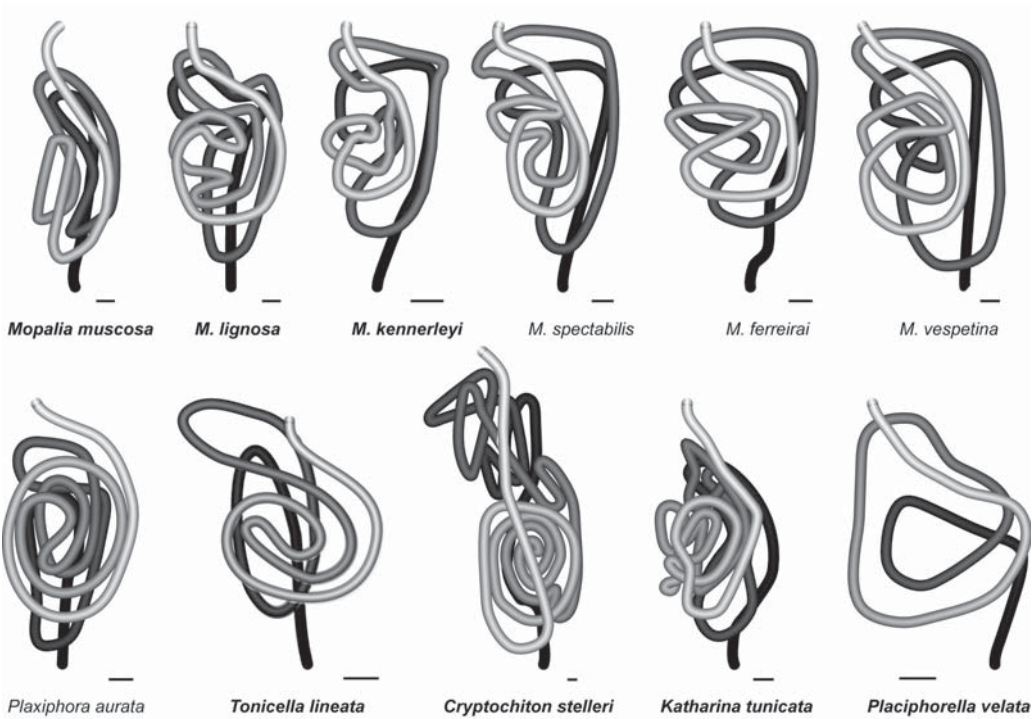


Fig. 1. Schematic drawings of the intestinal looping in 11 species of chitons in the superfamily Mopalioidae. In each schematic, the shading is graded light to dark from anterior to posterior; differently shaded areas are intended to illustrate multi-layered looping, they do not represent distinct parts of the gut. Species names in **bold type** are included in Fig. 2. Scale bars 2 mm.

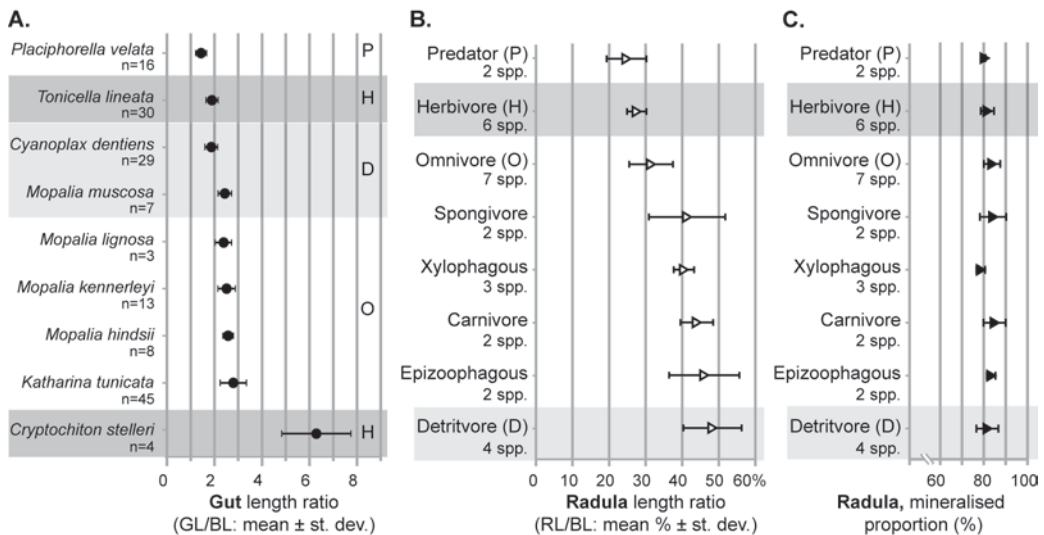


Fig. 2. Quantitative metrics of gut and radula morphology, in relation to feeding type. A —ratio of gut length to total individual body length, in 9 species where data were available for sufficient specimens. Letters at top and background shading correspond to feeding types shown in other parts. B —ratio of body length to radula length of multiple species within feeding types. C —proportion of mineralized teeth as a percentage of total tooth rows in the radula of multiple species within feeding types.

Visual representations are given for a few additional species for comparisons (Fig. 1). Gut length is shortest in the predatory species, *Placiphorella velata* where the gut forms only a double loop, and longest in the obligate herbivore *Cryptochiton stelleri* (intestinal length up to $>8 \times$ the body length). All other species are intermediate in length but closer in ratio value to *Placiphorella*; the herbivore *Tonicella lineata*, which feeds on coralline algae, had a gut / body length ratio that was not substantially higher than that for *Placiphorella* (Fig. 2A). The highest ratio apart from *Cryptochiton* was found in *Katharina tunicata*.

Our preliminary observations of radula metrics show a similar trend. Most species had very similar ratio values except for elevated ratios in known herbivores, omnivores, and predators (Table 1). Notably, the actively predatory species had higher relative radular length than other feeding types, and markedly higher than that for carnivorous grazers (Fig. 2B). The proportion of the radula that shows mineralisation was mostly invariant among all feeding types, though slightly lower in xylophagous and detritivorous

species (Fig. 2C). The potential importance of the ratio between the lengths of the radula to the supporting cartilage cannot be evaluated from the current data. The strong heterogeneity in the range of values (Table 1), even among the same feeding class, does not allow a statement about their significance. Further detailed studies expanding the sampling of these metrics, in combination with other methods (e.g., stable isotopes, fatty acid analysis) may provide a clearer signal.

Discussion

The wealth of literature on chiton ecology has already demonstrated that chitons use a variety of feeding strategies, and that feeding specialisms may be a key factor in the species-level evolution of modern chitons (Sirenko, 2000, 2004). However, chitons are superficially similar in their external morphology, so it is interesting to consider which aspects of anatomy are changed, or not changed, in correlation with these different feeding strategies.

The radula of chitons seems to vary with respect to some generalised feeding types. Most

interestingly, the total radula length as a proportion of body length is shortest in the predatory species examined, markedly shorter than for carnivorous grazing species. This suggests different feeding habits may be correlated with different patterns of radular wear and replacement. However, these preliminary data must be considered with caution. We examined only a single adult specimen of each species included. Saito (2004) pointed out that the variability in chiton radulae depends on the growth stage, and that is why we present only taxa where adult specimens were available. Nevertheless, special features of the radula are thought to be linked to particular feeding strategies. The most prominent tooth, the mineralised second lateral, shows not only a varying denticulation among taxa, but also a variable mixture of hardening elements (van der Wal et al., 2000). The different forms of the central tooth also indicate that their different morphology is linked to feeding processes. The third uncinial tooth might additionally play a greater role in food-uptake as “sweeper” teeth. While this tooth is usually slender and smooth, or sometimes reduced like in *Cryptochiton stelleri*, species with complete different feeding strategies for example the xylophagous *Ferreiraella* and the herbivorous *Tonicella squamigera* Thiele, 1909 (according to Sirenko, Scarlato, 1983) share a convergent broad, strongly pectinated third uncinial tooth though these taxa are in deeply separated clades.

The total number of rows in the radula can potentially vary by up to 20% around the population mean; Sigwart and Carey (2014) recorded 50 ± 10 tooth rows in a sample of adult specimens of *Leptochiton asellus* (Gmelin, 1791). Although data from that study showed the proportion of mineralised teeth was generally consistent, the proportion of mineralised teeth varied among individual chitons (Sigwart, Carey, unpub. results). Knowing that each species may be rather variable underscores the likely strong similarity in comparing across species in different feeding types; the differences we recorded (Fig. 2C) could be within the realm of individual variation. Therefore we suggest that the proportion of iron mineralised teeth is generally con-

sistent in all chitons, even those that live habitats such as sunken wood and may never encounter rocky substrata.

Our data show a very slightly lower level of mineralisation in the sampled xylophagous species, which may or may not represent a real biological trend. Some early fossils allied to modern chitons are morphologically similar to living species endemic to sunken wood, and wood habitats were apparently important in the radiation of living chitons (Sirenko, 2004). However, this does not contradict an interpretation that the mineralisation was adaptive in an ancestral chiton was for grazing on hard substrate. Time-calibrated phylogenetic reconstruction of living species suggests there have been multiple colonisations of sunken wood habitats by chitons (Sigwart, 2016). Even among xylophagous species that have apparently descended from wood endemic ancestors, there are substantial differences in feeding and digestion (Duperron et al., 2013). Continuing arrival of new lineages into wood habitats, and ongoing radiation within that ecosystem, may explain the conservation of iron mineralisation in the radula at the same rates as species on rocky shores.

Although the radula/body length ratio is not apparently diagnostic of feeding types, in particular differentiating the feeding types observed among species in Mopalioida, the ratio value could potentially predict the exclusion of some feeding strategies where ecological information is unavailable.

The evolution of these varied feeding strategies among chitons provides an interesting case study for morphological evolution. Changes in digestive anatomy, an in particular gut length, are well documented in a range of vertebrate taxa (Young, 1950). Predators have relatively short intestinal lengths while herbivores and particularly ruminants have extensively coiled elongate digestive tracts, though these trophic types are generally accompanied by obvious outward morphological differences. The case of the predatory chitons is therefore of particular interest: these predators are presumed to subsist on a diet of entirely animal food (McLean, 1962). In *Placiphorella velata*, the

characteristic extension on the anterior girdle used for trapping prey is present in juvenile animals, so it can be assumed that they maintain this mode of life throughout post settlement ontogeny. Yet the animals are sessile and have an extremely low metabolism (Carey et al., 2013). The gut of *Placiphorella velata* is shortened, and more importantly highly simplified in morphology to two overlapping simple clockwise loops, which take up very little space in the visceral mass. This is in line with what would be predicted for a predatory species.

Herbivorous chiton taxa include species that feed on seaweed, such as *Cryptochiton* (MacGinitie, MacGinitie, 1968), as well as species that graze encrusting coralline algae such as *Tonicella lineata*, which feeds largely on *Lithothamnion* (Piercy, 1987). We observe that herbivorous species seem to share a characteristic flat spiral coiling morphology in the intestine (Fig. 1: *Cryptochiton stelleri*, *Tonicella lineata*, *Placiphora aurata*). However, this is not quantitatively reflected in the relative size of gut length and body size (Fig. 2A). Previous work on patellogastropod limpets demonstrated that carnivorous species and obligate coralline feeders shared similar intestinal morphology (Lindberg, 1988). The same pattern is seen here in comparing the relative intestinal lengths of the chitons *Tonicella*, a coralline algae feeder, and *Placiphorella*, a predator. Interestingly, *Cyanoplax dentiens* feeds almost exclusively on diatoms (Piercy 1987), and also shows a similarly shortened gut length.

Katharina tunicata is typically referred to as an herbivore, with a preference for *Hedophyllum* (Himmelman, Carefoot, 1975) and the species has been shown to graze at rates that substantially affect local algal biomass (Dethier, Duggins, 1984). But those same authors also reported that the animals “appear to consume practically whatever they encounter” (Dethier, Duggins, 1984: 206). We observe that the intestinal morphology, though somewhat elongate in comparison to other chitons examined, the relative gut length is not very different to omnivorous species and does not have the characteristic flat concentric spiral seen in the other herbivo-

rous taxa we examined. This seems to correlate with a mixed diet for *Katharina*.

Several species in the genus *Mopalia* have previously been noted as omnivorous browsers. We examined several species in this genus, and all had similar intestinal coiling patterns. The ratio of body length to gut length is equivalent in all taxa, but there are some distinctive morphological differences. Coiling in *Mopalia muscosa* is much simpler, composed of seven elongate looping sections, whereas all other species of *Mopalia* have laterally extended loops that incorporate smaller doubling-back sections.

The differences in gut morphology have been described by previous authors (Plate, 1899, 1901; Fretter, 1937; Risbec, 1946; Saito, Okutani, 1992; Brooker, 2003; Sirenko, 2004). While these features have not been frequently used in taxonomic descriptions of chitons, their future use is encouraged. In patellogastropod limpets gut coiling has been commonly used in systematics (Walker, 1968), and led to the observation that more recently derived lineages tend to have more simplified intestinal morphology (Lindberg, 1988). Our evidence suggests this may also be the case in mopaliid chitons, as the genus *Mopalia* with its shorter omnivore gut is in a derived position relative to *Cryptochiton* and *Katharina* with longer and more complex guts (Kelly, Eernisse 2007; Sigwart et al., 2013). However, both carnivory and strict herbivory represent specialisms that may have evolved separately within this clade as derived lifestyles with corresponding adaptation to the gut, from a common ancestor in the past 30–40 million years.

Chitons are locally important grazers that exert significant control on algal resources (Littler, Littler, 1999), and indirectly facilitate accessibility of other food resources for additional grazing species (Dethier, Duggins, 1984). Within species, the use of different food resources apparently varies seasonally (Johns et al., 1980). If chitons are assumed to be ecologically similar, this suggests they may be competing for the same food and space resources. However, we know that many species of chitons co-occur. Certainly some co-occurring chitons have very different feeding strategies (Duperron et al.,

2013). The demonstrated flexibility of some chitons to shift between animal- or plant-based diets (Camus et al., 2009, 2013) may be advantageous to opening up ecological niche spaces within the same habitat.

Co-occurrence is observed at the level of individual organisms, but usually the ranges of the whole species are not entirely overlapping. This has been shown in chitons, where species that live together in certain sites have shell features that enable them to exploit different niches (Sigwart et al., 2015). In terms of feeding, chitons may be generalist browsers at the species level, and individually capable of digesting both animal and plant-based food. At smaller spatial scales, individuals or populations may be driven to specialise on particular diets based on variation in seasonal availability or the competitive impacts of other grazers including chitons. It is not clear to what extent omnivorous species, such as those studied here, are opportunistic grazers that consume any edible encrustation, or whether they are selecting specific prey.

The results of the present study confirm morphological differences in the gut that are correlated with feeding types and the shortening of the intestine in predatory and coralline-algae specialists. And there are morphological differences that are apparently distinct to species even within the same genus such as *Mopalia*. Future work on the diet of these omnivorous chitons may explain whether differential feeding preferences separate the niches for co-occurring species.

Acknowledgements

We thank Dr Nick Carey and Aaron Owens (Queen's University Belfast, Marine Laboratory) for assistance with lab work. This work was supported by the European Commission (award H2020-MSCA-IF-2014-655661 to JDS) and the Royal BC Museum, Canada.

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Responsible editor E.N. Temereva